

Productivity in Great Plains acid soils of wheat genotypes selected for aluminium tolerance

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Abstract

Soil acidity in the Great Plains of the USA can reduce forage and grain yields of winter wheat, primarily by Al toxicity. Indigenous cultivars may vary in seedling tolerance to Al toxicity, but the benefit that Al tolerance provides to forage and grain production is not well documented in this region. Backcrossed-derived lines of 'Chisholm' and 'Century' were selected with an additional gene from 'Atlas 66' conferring Al tolerance in solution culture. Our objective was to determine the impact of this source of Al tolerance on forage production prior to the jointing stage and subsequent grain yield. Experiments were conducted at several locations on non-limed (pH=4.5–4.7) and limed soils (pH=5.2–6.1) in Oklahoma. Two cultivars ('TAM 105', susceptible; '2180', tolerant) with extreme differences in Al tolerance were used as controls. In limed conditions, forage and grain production did not differ between Al-tolerant and -susceptible genotypes, indicating a neutral effect of the Atlas 66 gene in the absence of Al toxicity. Despite visual differences in early-season plant vigor in non-limed acid soil, the Al-tolerant selections did not yield greater season-long forage than their susceptible parents. At sites where Al saturation in the non-limed soil exceeded 30%, spike production at maturity was nearly doubled in the Century background by the addition of Al tolerance, but final grain yield was not significantly improved. In the Chisholm background, grain yield was improved 50 to 74% by Al tolerance. The magnitude of the agronomic benefit of Al tolerance was highly influenced by the edaphic environment and genetic background. Acid soils of the Great Plains appear highly variable in Al toxicity; hence, consideration of the target environment is essential to predict the potential impact of Al tolerance selected in solution culture.

Introduction

Genetic variability exists among the cereal species for tolerance to acidic soils (pH<5.5), where common wheat (*Triticum aestivum* L. em Thell.) is less tolerant than rye (*Secale cereale* L.) but more tolerant than durum wheat (*T. durum* L.) (Bona et al., 1995). Aside from managing soils for reduced rate of acidification, genetic improvement of acid soil tolerance, particularly Al tolerance, is one form of management.

Sufficient genetic variation occurs within the species but has been relatively underexploited in hard red winter (HRW) wheat produced in the Great Plains of the USA (Carver et al., 1988).

Production practices and land-lease commitments unique to the Great Plains have inspired interest in HRW cultivars with improved acid soil tolerance. Soil acidification caused by base depletion and nitrification of added ammoniacal N is accentuated in vast areas of Oklahoma, Texas, and Kansas, where the wheat crop is harvested for forage and grain in the same season. To compound this problem, producers often lease land on short-term contract and opt out of the long-term investment of lime application. Although soil acidity

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is generally limited to the surface layer (top 15 cm) and would appear rectifiable by lime application, the costs of transporting lime to areas in need far exceed the cost of the material. The critical need exists for HRW cultivars with improved grain and forage yield in acid soils, which will reduce lime requirements to more affordable levels.

Aluminum toxicity is traditionally recognized as a growth-limiting factor in acidic soils of Oklahoma, and elsewhere in the southeastern USA. Thus, selection is targeted toward genes conferring tolerance to Al, located on chromosomes of the A and D genomes (see ref. cited by Carver and Ownby, 1995, Table IV). Riede and Anderson (1996) located a gene on 4DL with relatively large effects on root growth of young seedlings under tightly controlled environmental conditions. Similar results with presumably other gene sources were reported by Aniol (1990).

A single gene for Al tolerance, transferred from Atlas 66 to HRW cultivars Chisholm and Century, increased seedling root growth in acidic Appalachian soils by 19 to 38% (Johnson et al., 1996). Dose responses also indicated a dramatic and qualitative effect of the gene on seedling root growth in solution culture. To be of any practical significance, however, gene expression must be verified in juvenile or adult plants grown in the target (low pH) set of production environments. Different genetic systems for Al tolerance could conceivably prevail in seedling versus adult plants, or in laboratory versus field environments.

Our objective was to determine the impact of Al tolerance on forage and grain produced in the same season under naturally acidic field conditions in Oklahoma. A forage-plus-grain production system is common to central Oklahoma, where soil acidity is prevalent. This study featured genetic stocks selected for similar genetic composition but differing for Al tolerance in solution culture. The impact of Al tolerance is more precisely determined in this type of material, rather than unrelated cultivars chosen for divergent Al response.

Materials and methods

The experimental materials comprised two HRW recurrent parents, Chisholm and Century, and two Al-tolerant backcross-derived lines from each of these parents (Carver et al., 1993). Each pair were BC₃F₂-derived sister lines in the F₆ generation, having approximately 94% of their genome in common with their

corresponding recurrent parent. The donor parent was Atlas 66, known for its Al tolerance (Berzonsky, 1992). Two check cultivars, TAM 105 and 2180, represented extreme levels of Al sensitivity and tolerance, respectively, currently known in HRW wheat.

Field experiments were conducted in the 1993-1994 and 1994-1995 seasons on research stations at three locations: Haskell, Lahoma, and Stillwater, Oklahoma. These locations represent major wheat growing areas in eastern and north central Oklahoma where acid soil conditions persist. A limed field site was also established at each location by incorporating lime to raise the soil pH to levels not considered limiting to yield. Thus, each location had two treatments, limed and non-limed, applied to adjacent areas of the field. The experimental design in each treatment-location was a randomized complete block with 10 genotypes (six backcross-derived lines, two recurrent parents, and two check cultivars) and three replicates. Plot size was 3.6 m² at all sites, comprised of five 3.0-m rows spaced 23 cm apart.

Planting dates (early September) and seeding rates (11 g m⁻²) conformed to standard production practices for a forage-plus-grain production system at Lahoma and Stillwater. Planting at Haskell was delayed until early October by excessive rainfall, preventing measurement of forage yield. Two additional sites were used only in the 1994-1995 season: a non-limed site near Enid, OK, where forage was removed one time but forage yield was not measured, and an additional limed site at Lahoma where the crop was managed for grain production only (planted in mid-October). The plot area was fertilized prior to planting according to soil-test recommendations to provide a minimum 100 kg N ha⁻¹, 67 kg available P ha⁻¹, and 270 kg available K ha⁻¹.

Forage was harvested with hand clippers about 5 cm above the soil surface from a 0.6 m² interior portion of each plot, at least once in the fall (more than 6 weeks after planting) and once in the spring before jointing. Clipping ceased in the spring before growing points of any entry in the test reached cutting height. Forage was collected from non-limed and limed plots on the same day, whenever canopy height in the non-limed plots allowed forage removal at 5 cm above the soil surface. The unclipped portion of the plot area was cut to a uniform 5-cm height with a rotary mower after each harvest. Samples were oven-dried at 50 to 55 °C for three days and weighed. Fall and spring measurements were combined to estimate total forage yield prior to jointing.

Grain yield and yield components were determined from the three interior rows. The number of spikes in a random 50-cm section of two interior rows was determined and reported as spikes m^{-2} . The number of kernels per spike and kernel weight were determined from 15 spikes randomly sampled from the interior rows of each plot.

Chemical analyses were conducted on bulk soil samples collected from each site (top 15 cm, limed and non-limed treatments), except the grain-only site at Lahoma where properties were expected to be similar to the Lahoma limed site. Enough soil was collected throughout the plot area to provide a 0.9 kg bulk. Soil pH was measured in 1:1 soil:H₂O and 1:1 soil:0.01 M CaCl₂ solutions. Bray P was determined in 2 g soil with 20 mL extraction solution (0.25 M HCl + 0.03 M NH₄F) according to Olsen and Sommers (1982). Exchangeable bases (Na, K, Ca, Mg, Mn) were extracted by 1 M NH₄OAc (pH 7), whereas exchangeable acidity (Al + H) was determined in 1 M KCl (Thomas, 1982). Extractable Al was determined by ICP after extracting soil with 0.01 M CaCl₂. Effective cation exchange capacity (ECEC) equaled the sum of K, Ca, Mg, Mn, Al, and H, and Al saturation equaled (Al/ECEC) \times 100, where values of elements and ECEC are in $\text{cmol}(+)\text{kg}^{-1}$.

Statistical analyses focused on the *F*-test of means comparisons between each susceptible parent and corresponding pair of tolerant derivatives, and between TAM 105 and 2180. Data for the two tolerant lines from each cultivar were combined due to similarity in response. For the low-pH sites, means were calculated across years, but within each location due to potential differences in Al phytotoxicity. Locations and years for the limed trials were considered a sample of the target population of environments unlimited by acid soils, so means were reported across location-years. Variability in soil pH was closely monitored among individual plots. Three soil cores (top 15–20 cm) were collected from each plot in May to determine pH before harvest. These values were used in an analysis of covariance. For a few traits from the non-limed sites, the covariate provided a significant reduction in experimental error variance. Inclusion of the covariate in the model, however, provided only modest reductions in CV and no qualitative change in the means comparisons based on least-squares estimates. Hence, only the unadjusted means were reported.

Results

The non-limed sites were consistent in pH(H₂O), and 0.7 to 1.4 units lower than the corresponding limed sites (Table 1). Lime application resulted in low levels of exchangeable and extractable Al. None of the limed sites was considered Al-phytotoxic based on Al saturation, although additional lime would have been necessary at the Haskell site to completely eliminate exchangeable Al. The non-limed sites were variable for potential Al phytotoxicity, ranging from higher levels (>30% Al saturation) at Haskell and Enid to lower levels (<16% Al saturation) at Stillwater and Lahoma. Manganese concentration was relatively high in the non-limed treatment at Lahoma, while Ca concentration was relatively high in the non-limed treatment at Stillwater. Values of ECEC were similar to those reported for a large number of acid soils in central tropical South America (Cochran et al., 1985).

Under limed conditions, the amount of forage produced by the Al-tolerant genotypes did not change relative to their susceptible counterparts, including the comparison of check cultivars (Table 2). With one exception, the susceptible and tolerant selections also followed similar patterns in spike production and grain yield, with no difference in other yield components (seeds per spike or kernel weight, not shown). Thus, in the absence of Al toxicity, total agronomic performance with respect to forage and grain was unaffected by the genetic capacity to tolerate Al toxicity.

Forage yield was reduced markedly at the low-pH sites. TAM 105, the most sensitive genotype to soil acidity for total forage yield (Table 3), produced no measureable early-season forage during the fall at either location. Among all genotypes, the tolerant check cultivar, 2180, produced the most forage, but its yield under low pH was still only one-half of its yield potential under limed conditions (Table 2). Despite a trend toward higher yield, the Al-tolerant selections of Chisholm and Century did not significantly exceed their susceptible parents in total forage production prior to the jointing stage. The tolerant selections did show obvious improvement in plant vigor soon after emergence, but visual differences became less noticeable as the season progressed.

The number of spikes counted at maturity (harvest) represents the net effect of tiller formation and tiller survival. Reduced tiller formation in the non-limed treatments was reflected, in part, by reduced forage yields. Using the Al-sensitive check, TAM 105, as a gauge for acid soil stress, spike production was

Table 1. Selected soil properties for three limed and four unlimed field sites in Oklahoma

Site ^c	pH (H ₂ O) ^d	pH (CaCl ₂) ^d	Bray P (mg ⁻¹ kg)	CEC (cmol kg ⁻¹)	Exchangeable ^a					Extractable ^b		Al satur- ation (%)
					Mg	Ca	Mn	Acidity	Al	Al		
Stillwater, limed	6.1	5.7	42.5	9.3	3.1	5.7	0.02	0.06	0.03	<0.01		0.3
Lahoma, limed	5.6	5.0	101.8	9.3	2.0	5.7	0.05	0.07	0.03	<0.01		0.3
Haskell, limed	5.2	4.5	22.9	4.2	0.5	3.4	0.06	0.34	0.23	0.01		5.2
Stillwater, non-limed	4.7	4.2	59.9	7.8	1.9	4.1	0.09	1.20	0.95	0.03		12.2
Lahoma, non-limed	4.5	4.0	70.8	5.9	1.2	2.3	0.27	1.20	0.91	0.04		15.5
Haskell, non-limed	4.5	3.8	46.1	3.4	0.2	1.1	0.15	1.57	1.11	0.12		32.3
Enid, non-limed	4.5	3.9	64.4	3.4	0.3	1.5	0.05	1.26	1.09	0.08		31.8

^a 1 *N* NH₄OAc extractant for Ca, Mg, and Mn and 1 *M* KCl extractant for exchange acidity (Al, H).

^b Extractable by 0.01 *M* CaCl₂.

^c Stillwater soil, Bethany-Kirkland complex (Pachic- Udertic Paleustoll); Lahoma and Enid soils, Pond Creek silt loam (Pachic Argiustoll); Haskell soil, Taloka silt loam (Mollic Albaqualf).

^d 1:1 soil:solution volume (w/v).

Table 2. Forage and grain production for two Al-tolerant selections and their recurrent parents, and two check cultivars, averaged across five limed environments (four environments for forage yield)

Genotype	Forage yield (g m ⁻²)	Spikes (no. m ⁻²)	Grain yield (g m ⁻²)
Chisholm ^a	256	769	169
Chisholm-T ^b	259	743	154
F-test	NS	NS	NS
Century ^a	252	724	130
Century-T ^b	276	806	119
F-test	NS	*	NS
TAM 105 ^c	270	875	145
2180 ^c	248	671	168
F-test	NS	**	NS

^a Recurrent parents.

^b Al-tolerant backcrossed-derived selections.

^c Control cultivars.

most restricted at Haskell and Enid, where Al saturation was the highest (Table 4). At those locations, the Al-tolerant Century-T selection produced nearly twice as many spikes as Century. The increase in spike production of Chisholm-T compared to Chisholm was not significant. Neither of the Al-tolerant selections showed a significant improvement in spike production at Lahoma, although spike production of 2180 doubled that of TAM 105. At Stillwater, the Al-tolerant genotypes, Chisholm-T and 2180, actually produced fewer spikes than their susceptible counterparts. Another

Table 3. Forage yields for two Al-tolerant selections and their recurrent parents, and two check cultivars, averaged across two years at two locations under low soil pH (non-limed) conditions

Genotype	Stillwater Lahoma	
	(g m ⁻²)	
Chisholm	74	46
Chisholm-T	74	94
F-test	NS	NS
Century	59	39
Century-T	76	95
F-test	NS	NS
TAM 105	38	20
2180	105	143
F-test	**	**

unusual feature of this low-pH site was that the three sensitive cultivars (Chisholm, Century, and TAM 105) showed the smallest reduction in spike number from the limed treatment (659 spikes m⁻²) to the non-limed treatment (614 spikes m⁻², Table 4).

Differences in grain yield between susceptible and Al-tolerant genotypes paralleled those in spike production. The widest genetic differences associated with Al tolerance were observed in Haskell and Enid, where grain production of TAM 105 was severely limited (Table 5). Overall, the Al-tolerant Chisholm-T selection showed a 50 to 74% grain yield advantage relative to Chisholm. The higher spike production of Century-

Table 4. Spike production for two Al-tolerant selections and their recurrent parents, and two check cultivars, averaged across two years at three locations (one year at Enid) under low soil pH (non-limed) conditions

Genotype	Stillwater	Lahoma	Haskell	Enid
	(spikes m ⁻²)			
Chisholm	601	670	263	589
Chisholm-T	537	688	363	628
F-test	*	NS	NS	NS
Century	637	736	229	447
Century-T	592	747	429	801
F-test	NS	NS	**	**
TAM 105	604	323	136	136
2180	499	686	428	621
F-test	**	*	**	**

Table 5. Grain yield for two Al-tolerant selections and their recurrent parents, and two check cultivars, at four locations under low soil pH (non-limed) conditions

Genotype	Stillwater ^a	Lahoma ^b	Haskell ^a	Enid ^c
	(g m ⁻²)			
Chisholm	177	156	153	128
Chisholm-T	170	159	229	223
F-test	NS	NS	**	**
Century	176	163	152	155
Century-T	132	181	189	184
F-test	*	NS	NS	NS
TAM 105	166	61	32	0
2180	173	146	213	271
F-test	NS	**	**	**

^a Data from 1994 only.

^b Data averaged across 1994 and 1995.

^c Data from 1995 only.

T compared with Century (Table 4) did not translate into significantly higher grain yield at Haskell or Enid. At Haskell, the greater number of spikes of Century-T was offset by significantly fewer kernels per spike (15.9 vs. 26.8 kernels spike⁻¹), whereas the lack of a yield response at Enid could not be attributed to significant compensatory reductions in kernel number per spike or kernel weight (data not shown). No improvement in grain yield was associated with Al tolerance at Stillwater and Lahoma, except for the comparison between checks at Lahoma. Contrary to expectation, the Al-tolerant Century-T selection produced less grain yield than its susceptible parent in the non-limed treatment at Stillwater.

Discussion

Under limed conditions where Al phytotoxicity was virtually eliminated, the Atlas 66-derived gene conferring Al tolerance in solution culture did not alter yield of either forage or grain. Gene neutrality in the absence of Al toxicity is desirable where Al-tolerant cultivars might be extended beyond acid-soil environments. Neighboring fields ranging from severe to no Al toxicity are not uncommon in the Great Plains, depending on management practices of individual producers.

The low grain yields reported in this study can be attributed, in part, to the management system used to produce harvestable forage and grain in the same season. Winter and Thompson (1990) and Ud-Din et al. (1993) showed that forage removal can suppress subsequent grain yield in plots harvested for both forage (before jointing) and grain. In this study, grain yield suppression was accentuated in the limed plots, because greater forage production under limed conditions meant proportionately greater canopy depletion at jointing compared with non-limed conditions. Grain yield under limed conditions was also likely suppressed by the root rot diseases, sharp eyespot (incited by *Rhizoctonia* sp.) and take-all (incited by *Gaeumannomyces graminis* var. *tritici*) (Krenzer and Singleton, 1995). *Rhizoctonia* sp. were detected, and take-all symptoms were observed, in each of the locations used in this study. Symptom expression of these diseases was so severe in 1995 that grain yield at Stillwater and Haskell was excluded from analysis. An increase in disease pressure following lime application has been reported elsewhere (Murray et al., 1987).

The agronomic benefit of Al tolerance introduced from Atlas 66 into Chisholm or Century was evident in relatively Al-toxic environments (Enid and Haskell) but lacking in others where Al saturation was $\leq 12\%$ (Stillwater). The strong environmental effect was exemplified in the variation among locations in relative spike number (i.e., proportion of spikes in the non-limed treatment relative to spike number in the limed treatment), a trait largely unaffected by root rot diseases and forage removal before jointing. Averaged across years in decreasing order, relative spike number for the susceptible check, TAM 105, was 0.85 (Stillwater), 0.32 (Lahoma), and 0.23 (Haskell). Corresponding values for 2180 were 1.09, 0.98, and 0.98. Thus, between the two checks, Al tolerance was more difficult to detect in Stillwater than in Haskell, yet soil pH differed only by 0.2 units. A more detailed chemical analyses indicated that Al saturation, not soil pH,

dictated genotypic response. Aluminum saturation was more than two-fold higher at Haskell (and at Enid) than at Stillwater and Lahoma. Response to Al was possibly confounded or masked by elevated Mn content at Lahoma, while the higher Ca content at Stillwater could have partially reduced Al toxicity at that site. The Al-tolerant selections of Chisholm and Century are not known to have Mn tolerance given their recurrent parentage. Their donor parent, Atlas 66, is Mn sensitive (Foy et al., 1973).

In conclusion, we found the agronomic benefits of Al tolerance in Great Plains acid soils to be influenced by the edaphic environment and by genetic background; gene effects were generally neutral in the absence of acid-soil stress. Field sites with similar pH may produce vastly different results depending on Al saturation and other inherent soil chemical properties. Thus, consideration of the target production environment is essential in predicting the potential impact of single-gene doses of Al tolerance. The presence of root rot diseases in the limed experiments precluded estimation of the impact of Al tolerance based on relative grain yields in the non-limed and limed sites. Because forage yield was reduced markedly for both susceptible and tolerant genotypes in the non-limed sites compared to the limed sites, improvement in forage yield in acid soils would appear to be an even greater challenge than improvement in grain production.

The consistent superiority of 2180 relative to TAM 105 at all non-limed sites implies these genotypes were more genetically divergent for tolerance to Al or other soil factors than the backcross-derived tolerant selections and their parents. While some improvement may be expected from selection of "major" genes for Al tolerance, such as the one transferred from Atlas 66, selection for additional genes expressed under low soil pH in the target environment will be necessary to maximize acid soil tolerance in wheat.

References

- Aniol A 1990 Genetics of tolerance to aluminium in wheat *Triticum aestivum* L. Thell). Plant Soil 123, 223–27.
- Berzonsky W A 1992 The genomic inheritance of aluminum tolerance in 'Atlas 66' wheat. Genome 35, 689–693.
- Bona L, Baligar V C and Wright R J 1995 Soil acidity effects on agribotanical traits of durum and common wheat. In Plant and Soil Interactions at Low pH. Ed. R A Date et al. pp 425–428. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Carver B F, Inskeep W P, Wilson N P and Westerman R L 1988 Seedling tolerance to aluminum toxicity in hard red winter wheat germplasm. Crop Sci. 28, 463–467.
- Carver B F, Whitmore W E, Smith E L and Bona L 1993 Registration of four aluminum-tolerant winter wheat germplasms and two susceptible near-isolines. Crop Sci. 33, 1113–1114.
- Carver B F and Ownby J D 1995 Acid soil tolerance in wheat. Adv. Agron. 54, 117–173.
- Cochran T T, Sanchez L G, Azevedo L G, Porros J A and Garver C L 1985 Land in tropical America. Vol. 1. CIAT, Cali Columbia and EMBRAPA - CPAC, Planaltina, D.F. Brazil.
- Foy C D, Fleming A L and Schwartz J W 1973 Opposite aluminum and manganese tolerances of two wheat varieties. Agron. J. 65, 123–126.
- Johnson J P Jr, Carver B F, Baligar V C and Raun W R 1996 Expression of aluminum tolerance transferred from Atlas 66 to hard winter wheat. Crop Sci. 36 (In press).
- Krenzer G and Singleton L 1995 Root rots in wheat. Oklahoma Cooperative Ext. Serv. PT 95–15.
- Murray G M, Scott B J, Hochman Z and Butler B J 1987 Failure of liming to increase grain yield of wheat and triticale in acid soils may be due to the associated increase in incidence of take-all (*Gaeumannomyces graminis* var. *tritici*). Aust. J. Exp. Agric. 27, 411–417.
- Olsen S R and Sommers L E 1982 Phosphorus. In Methods of Soil Analysis. Part 2. Ed. A L Page. pp 403–430. Agron 9, ASA, SSSA, Madison, WI, USA.
- Riede C R and Anderson J A 1996 Linkage of RFLP markers to a wheat aluminum tolerance gene. Crop Sci. 36 (In press).
- Thomas G W 1982 Exchangeable cations. In Methods of Soil Analysis. Part 2. Ed. A L Page. pp 159–165. Agron 9, ASA, SSSA, Madison, WI, USA.
- Ud-Din N, Carver B F and Krenzer E G Jr 1993 Visual selection for forage yield in winter wheat. Crop Sci. 33, 41–45.
- Winter S R and Thompson E K 1990 Grazing winter wheat: I. Response of semidwarf cultivars to grain and grazed production systems. Agron. J. 82, 33–37.

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